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NEW OCCURRENCES OF THE WOOD *PROTOCUPRESSINOXYLON PURBECKENSIS* FRANCIS: IMPLICATIONS FOR TERRESTRIAL BIOMES IN SOUTHWESTERN EUROPE AT THE JURASSIC/CRETACEOUS BOUNDARY

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Abstract: Previously known from the Kimmeridgian–Portlandian of Dorset (UK) only, *Protocupressinoxylon purbeckensis* wood is reported here from the Kimmeridgian of Asturias (Spain) and Ajoie (Switzerland). The morphospecies taxonomy and nomenclature are discussed, and new supplementary illustrations are given. The *P. purbeckensis* tree was growing in dry strongly seasonal (tropophilous) environments, and the new occurrences suggest that such a climate prevailed on land all over southwestern Europe at the end of the Jurassic (Kimmeridgian *sensu anglico* – Portlandian). The review of fossil wood data indicates that such a stressful environment may have constrained terrestrial biocoenoses and their evolution at the Jurassic/Cretaceous boundary. But wood generic diversity curves are also strikingly similar to that drawn 20 years ago for nonmarine tetrapods, implying a fossil *Lagerstätte* effect.

Key words: Jurassic, Cretaceous, boundary, fossil wood, palaeoecology, southwestern Europe.

FOSSIL wood morphospecies have very patchy records, and those known from the Jurassic of Europe have rarely been mentioned more than once (Philippe 1995). The main exceptions are *Xenoxylon latiporosum* Gothan (an Arctic wood with occasional occurrences at lower latitudes) and *Simplicioxylon hungaricum* Andreanszky (widespread during the Liassic in southern Europe). This makes palaeobiogeographical syntheses at the morphospecies level difficult (Philippe *et al.* 2006).

While studying Late Jurassic fossil wood in Western Europe, we chanced several times upon a wood morphospecies, which has distinct characteristics. Its particular cross-field pitting makes it easy to recognize, despite some variability in the tracheid radial wall pitting. It was originally described by Francis (1983) from the Great Dirt Bed in the Isle of Portland and named by her *Protocupressinoxylon purbeckensis*.

Here, we report several new finds of *Protocupressinoxylon purbeckensis* Francis from Ajoie (Switzerland) and Asturias (Spain). The new specimens are briefly described, and new illustrations are given for this species. The species is of stratigraphical interest as its record is restricted to the Kimmeridgian–Tithonian interval. The species palaeoecology was determined, combining sedimentological and taphonomical observations. Finally, the significance of this wood in the more general context of wood flora evolution at the Jurassic/Cretaceous boundary is discussed.

NEW MATERIAL OF *PROTOCUPRESSINOXYLON PURBECKENSIS* FRANCIS

Geological framework

Spain. The Spanish material was found on the rocky beaches and in the cliffs between the localities Gijón and Ribadesella, along the coast of Asturias, northern Spain (Text-fig. 1), within a Jurassic sedimentary sequence

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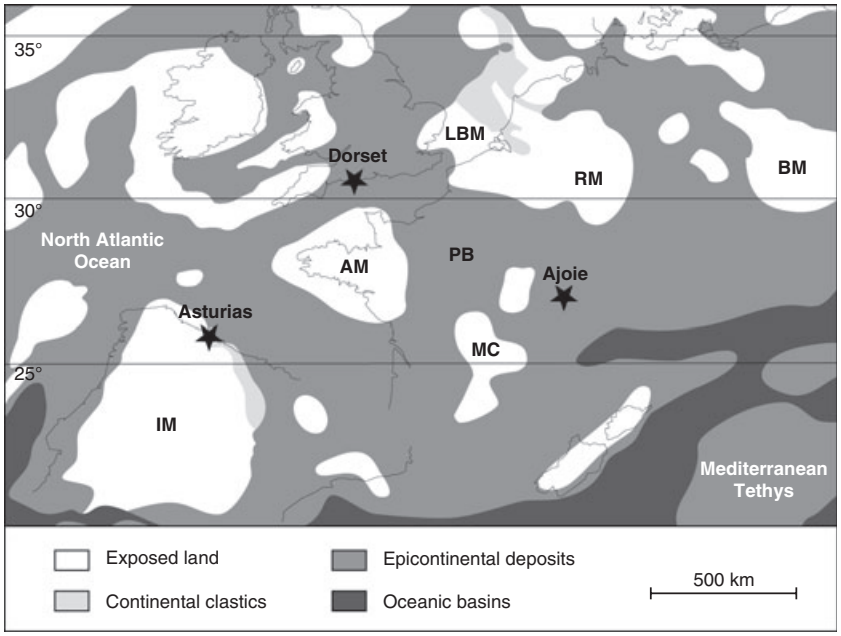


TEXT-FIG. 1. *Protocupressinoxylon purbeckensis* distribution. Early Kimmeridgian (Late Jurassic) palaeoenvironmental map of Western Europe after Thierry *et al.* (2000). Originally known exclusively from Southern England (Francis 1983; Abineri 1989) this taxon has also been documented from Northwestern Switzerland (Ajoie, Canton Jura) and Spain (Asturias) (this study). AM, Armorican Massif; BM, Bohemian Massif; IM, Iberian Massif; LBM, London Brabant Massif; MC, Massif Central; RM, Rhenish Massif; PB, Paris Basin.

topped by the Tereñes and Lastres formations, both dated as Kimmeridgian (all stage names according to international standard) on the basis of ammonite record (Dubar and Mouterde 1957; Suárez Vega 1974; Oloriz *et al.* 1988; Valenzuela *et al.* 1998; Aurell *et al.* 2003). According to Schudack and Schudack (2002*a*, *b*), analysing the ostracod record, the Asturias Upper Jurassic succession reaches the early Tithonian, but their sampling is not precise enough to fully support their conclusion.

The sedimentary sequence begins with the Vega Formation, a 150-m thick series of fluvial red beds. Deep vertical root traces and caliche palaeosols indicate that these rocks were deposited under semi-arid conditions with ephemeral fluvial activity. The overlying Tereñes Formation, about 150 m thick, may reflect a subsequent rise in sea level that led to extensive organic-rich marl deposition in a shallow, restricted and nontidal sea, protected on its outer margin by a structural swell (Aurell *et al.* 2002). Mudcracks, salt pseudomorphs and localized gypsum layers indicate periods of evaporation and repeated emergence in the early part of deposition.

The overlying Lastres Formation consists of about 400 m of grey sandstone, mudstone, marl and occasional conglomerate layers. Current ripples and sole marks are common indicators of unidirectional fluvial flow, and in some places *in situ* fossil-tree trunks, shell accumulations and well-preserved plant fossils indicate rapid deposition. The general setting of Lastres Formation is considered a fluvial-dominated deltaic system (García-Ramos *et al.* 2002, 2004, 2006). Fossil wood was collected from the Tereñes and Lastres formations.

Switzerland. The Swiss material was found in the Ajoie district, Northwestern Switzerland (Text-fig. 1), in subhorizontally layered Late Jurassic strata of the northern Tabular Jura (Swiss Jura Mountains). It was discovered in a marly calcareous sequence at Tchâfouè (TCH), near Courtedoux town (about 3 km west of Porrentruy, Ajoie, Canton Jura), during excavations for the Transjurane (A16) highway (Marty *et al.* 2003). This sequence was ascribed to the upper part of the Reuchenette Formation, a thick (40–180 m) carbonate platform succession (Thalmann 1966*a, b*; Gygi 2000*a, b*; Colombié and Strasser 2005). The wood-bearing level belongs to the Virgula Marls reported by Laubscher (1963) and the Virgula Member of Gygi (2000*a*, *b*) but strictly corresponds to the Virgula Marls *sensu* Jank *et al.* (2006*b*). These up to 1 m thick, beige or dark grey, glauconitic, oyster-rich (*Nanogyra nana*) marls are precisely dated as late Kimmeridgian (Eudoxus Zone) by ammonites (*Aspidoceras* cf. *longispinum*) (Jank *et al.* 2006*a*; Colombié and Rameil 2007; Marty *et al.* 2007, fig. 2). Along with wood remains, these marls have yielded a rich and diverse coastal marine assemblage of invertebrates (bivalves, gastropods, cephalo-

pods, crustaceans, echinoids) and vertebrates (chondrichthyes, osteichthyes, turtles, crocodylians), notably many plesiochelyid turtles (Billon-Bruyat 2005). The general depositional setting is considered a shallow subtidal, protected marine environment (Jank *et al.* 2006*b, c*).

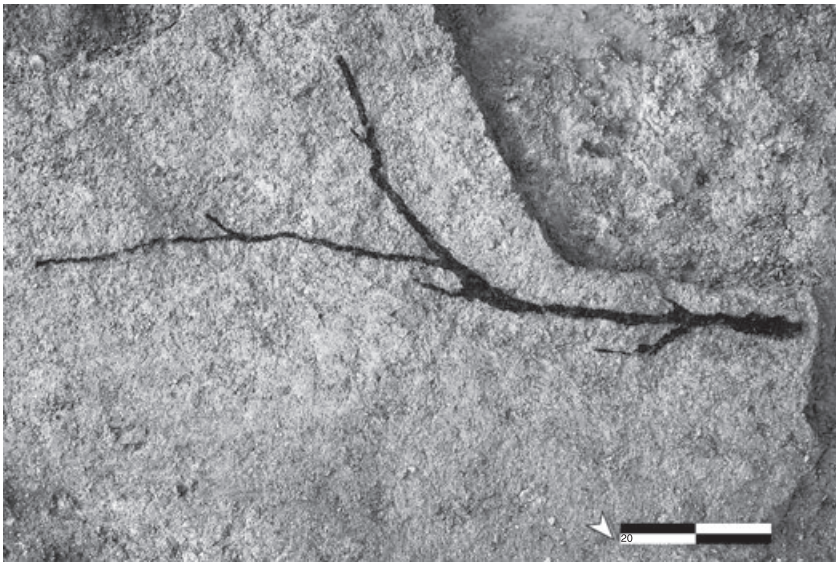
MATERIAL AND METHODS

Taphonomical observations. The Swiss specimens were all from slender axes (elongate linear vegetative structures), reaching up to 1.75 m in length. Most of them were sympodial (Text-fig. 2), with a bayonet-like growth building a succession of decimetric, slightly curved units. As this pattern was frequently observed, this was probably the normal growth pattern rather than the result of several traumatic events. Most of studied axes were branched (Text-fig. 3), and because of their growth mode and branching angles together with sub-planar disposition, these axes were probably branches rather than small trunks. The preservation, however, made it impossible to check the occurrence of compression wood. These branches were found to be similar to those of modern *Araucaria heterophylla* (Salisb.) Franco. The specimen size indicates that they originated from branches at least 3 m long, confirming Francis' reconstruction of the *Protocupressinoxylon purbeckensis* plant as a tree of some stature (20 m?, see Fitton 1836, p. 221; Francis 1983).

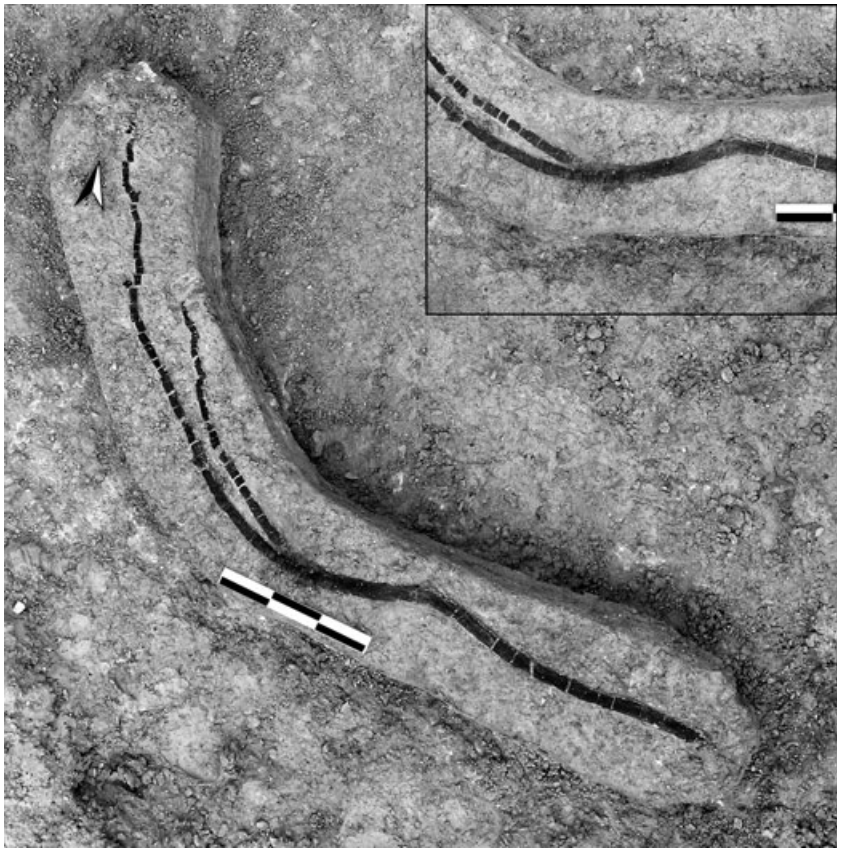
None of the Swiss fossils had blunt or rounded tips, and their branches were often well preserved (Text-fig. 3). This, together with the length of these woody axes, suggests that they were not transported for a long time. This was supported by these axes not being found associated with any fossilized epibionts. Infracentimetric and more or less isodiametric woody fragments were totally absent in the Swiss locality, whereas they are usually common elsewhere. These small fragments might have been winnowed by sea currents, as the setting was definitely marine, but the preserved wood axes displayed no preferential orientation on the whole (Text-fig. 4) and such currents would have also broken up the branches. Actually, we observed locally closely spaced and more or less unidirectional wood axes (Text-fig. 5), or accumulations of small woody fragments, but only in a marly bed situated about 0.8 m below the Virgula Marls. In addition, the wood axes are deposited on bedding planes, as were associated vertebrate remains. In conclusion, we hypothesize that these branches were broken off by strong winds, blown away, floated in the sea for a short while before being buried in a shallow epicontinental sea.

The fossil wood from Switzerland was preserved as lignite, whereas in Asturias specimens were mostly preserved as fusinite in sediments that formed in a deltaic setting (Valenzuela *et al.* 1998). It was recently shown that fusinite could result not only from wildfires, but possibly also from acid leaching during pedogenesis that takes place after exposure of anoxic reducing sediments (Gerards *et al.* 2007). The Spanish material cannot thus be used as evidence that wildfires occurred at that time in this area. Specimens were too broken and small to allow any interpretation on the morphology of the original axes. Most specimens were small, but they were apparently not size sorted. In contrast to Swiss material, information that can be drawn from the taphonomy of Spanish material is limited.

Study techniques. Samples were first sorted under a Wild M3Z stereomicroscope to select a study technique



TEXT-FIG. 2. Thin and branched woody axes are common in Ajoie (late Kimmeridgian, Jura, Switzerland). Sample MJSN SCR008-45, from the Virgula Marls of Courtedoux-Sur Combe Ronde, a locality close to Courtedoux-Tchâfouè. On the scale, each black bar is 10 cm long; the arrow points to the North.



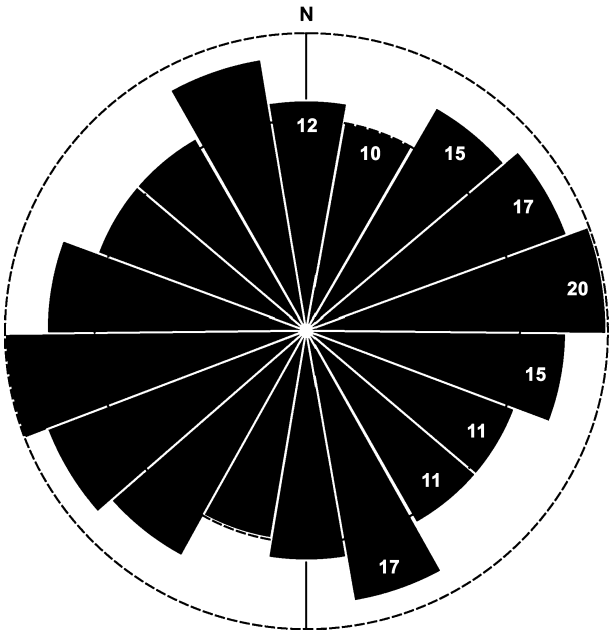
TEXT-FIG. 3. Swiss specimens (late Kimmeridgian) regularly display sympodial growth, i.e. a growth where apical meristem was consumed to make an apical (seemingly lateral) determinate structure, whereas branch growth was continued by a lateral (seemingly apical) meristem. Sample MJSN TCH005-660. On the scale, each black bar is 10 cm long; the arrow points to the North.

appropriate to the nature of their preservation style (lignite, fusinite). When mineralized, samples were searched for a fresh fracture in radial plan or, in the absence of such a surface, gently split with a disposable razor blade. On the fracture plan thick Collodion (cellulose acetate) was applied and allowed to dry for a day. The Collodion peel was then stripped off and studied with a normal transmitted light microscope. If not suitable for this technique, samples were mounted on aluminium stubs, with double-sided conducting adhesive tape, coated with gold/palladium at 25 kV for 5 min and then observed under a 10-kV acceleration voltage with a Hitachi S-800 scanning electronic microscope (SEM).

Institutional abbreviations. LPUL, Laboratoire de Paléobotanique de l'Université de Lyon, Université Lyon-1 (France); MJSN, Musée Jurassien des Sciences Naturelles, Porrentruy (Switzerland); MUJA, Museo del Jurásico de Asturias (Spain).

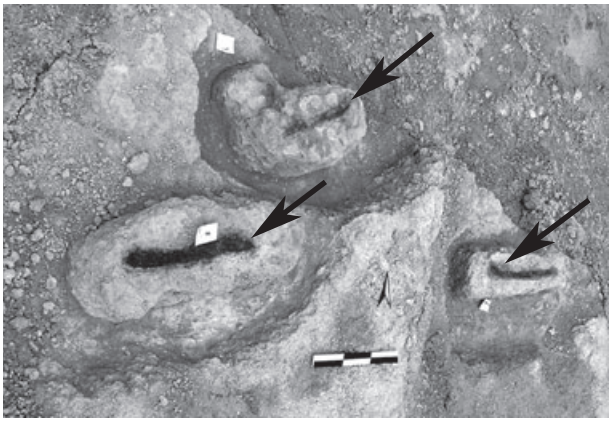
Material studied. More than 50 samples from Switzerland were preliminary examined. Seven were selected for further study (Table 1). From the Spanish sequences, we examined six samples (Table 1), four of which are well preserved and used in this study. Samples MP1631 and MP1632 are from the Tereñes Fm, and MP1630 and MP1633 are from the younger Lastres Fm. All described material is kept in the collections of MJSN (Switzerland) and MUJA (Spain), respectively, SEM stubs being stored in LPUL (France).

A database for the Jurassic/Cretaceous boundary. To interpret these new occurrences in a palaeoecological perspective, we compiled all wood data from the Jurassic/Cretaceous boundary of southwestern Europe into a single database. We selected the Late Oxfordian – Berriasian interval as it corresponds to a period of little floristic turnover (Philippe *et al.* 1999) with a rather uniform green-house climate, after the cooling event which occurred during the Late Callovian – Early Oxfordian (Dromart *et al.* 2003) and before the switch to a much more wet climate, which took place at the end of the Berriasian (Gröcke *et al.* 2003; Schnyder *et al.* 2005*b*, 2006). About fifty occurrences (Late Oxfordian, n = 9;



TEXT-FIG. 4. Rose plot of the orientations of 128 wood axes from the late Kimmeridgian of Courtedoux-Tchâfouè (Ajoie, Jura, Switzerland). The specimens have been excavated on a large surface (about 2350 m^2) in the 1-m thick Virgula Marls (*sensu* Jank *et al.* 2006*a*). As seen in this diagram, the wood axes are randomly oriented on the whole, as confirmed by a nonsignificant result of a chi-square test (at $p < 0.01$). This is an equal-area rose plot with bins equalling 20 degrees, created with the software PAST (Hammer and Harper 2006).

Kimmeridgian, n = 21; Tithonian, n = 13; Berriasian, n = 5) were gathered, either from literature or as personal unpublished data.



TEXT-FIG. 5. Three closely spaced and almost parallel wood axes (black arrows) with a preferential E–W direction at Courtedoux-Tchâfouè (late Kimmeridgian, Ajoie, Switzerland, Samples TCH005-95, -101, -127. On the scale, each black bar is 10 cm long; the black and white arrow points to the North.

PALAEOXYLOGICAL RESULTS

Wood anatomy description. All the samples of the Spanish material were found to belong to the same type of wood (Text-fig. 6), and they are thus described collectively: a secondary pycnoxylic xylem, composed only of tracheids with some occasional axial parenchyma; in transverse section growth-rings present, indistinct, with only a small amount of poorly differentiated late wood; no resin canals observed; in tangential section rays mostly low, ranging in height from 2 (rarely one) to 6 (rarely up to 7) cells; all observed rays uniseriate; on tracheid radial wall pitting of mixed type, mostly araucarian, more than 84% of observed radial pits (n = 152) being uniseriate and contiguous, 11% being uniseriate but slightly distant from neighbouring pits, 4% being biseriate alternate to sub-opposite; axial parenchyma was observed at one place in radial section, with smooth transversal wall; ray parenchyma cells smooth and thin walled, unpitted except for the cross-fields; in the early wood cross-fields variable, featuring one to six oculipores; when single, the oculipore markedly larger, occupying almost all of the cross-field; oculipores cupressoid, i.e. with a narrow slit-like aperture which does not reach the edge of the areola; in cross-fields with more than one pit, three to five oculipores, sometimes up to seven, with contiguous and alternate arrangement (araucarioid disposition); oculipores more numerous in marginal and external cells than in those in the middle of the ray; in the late wood, cross-field pitting

TABLE 1. Studied material.

Institutional abbreviations	No MP	SEM stub number	Collodion technique used
Swiss material			
MJSN TCH005-322	MP1701	422	No
MJSN TCH006-334	MP1702	None	No
MJSN TCH006-755	MP1703	None	Yes
MJSN TCH005-107	MP1704	422	No
MJSN TCH006-355	MP1705	421	No
MJSN TCH006-130	MP1706	420	No
MJSN TCH005-94	MP1707	421	No
Spanish material			
JT-20	MP1630	MP393	No
JT-20	MP1630	MP394	No
JT-20	MP1630	MP396	No
Muja 0644+ JA14	MP1631	MP395	No
Exposicion	MP1632	None	Yes
JA14	MP1633	None	Yes

MJSN, Musée Jurassien des Sciences Naturelles, Porrentruy (Switzerland); No MP, study record number in Laboratoire de Paléobotanique de l'Université de Lyon; SEM, scanning electronic microscopy.

less variable, usually with only 2–3 contiguous cupressoid oculipores.

The Swiss samples studied did not differ significantly from the Spanish material (Text-fig. 6F–G). Observed ray heights range from 1 to 9 cells. On tracheid radial walls, pitting was also of mixed type, albeit slightly more araucarian than the Spanish samples with about 92% of observed radial pits (n = 78) uniseriate and contiguous, 4% uniseriate but slightly distant from neighbouring pits and 4% biseriate alternate (rarely sub-opposite). Axial parenchyma was not observed in radial sections, but this might be as a result of preservation. Similarly, early wood cross-fields were variable, featuring one to seven oculipores, with single oculipores being much larger in size, as in the Spanish material.

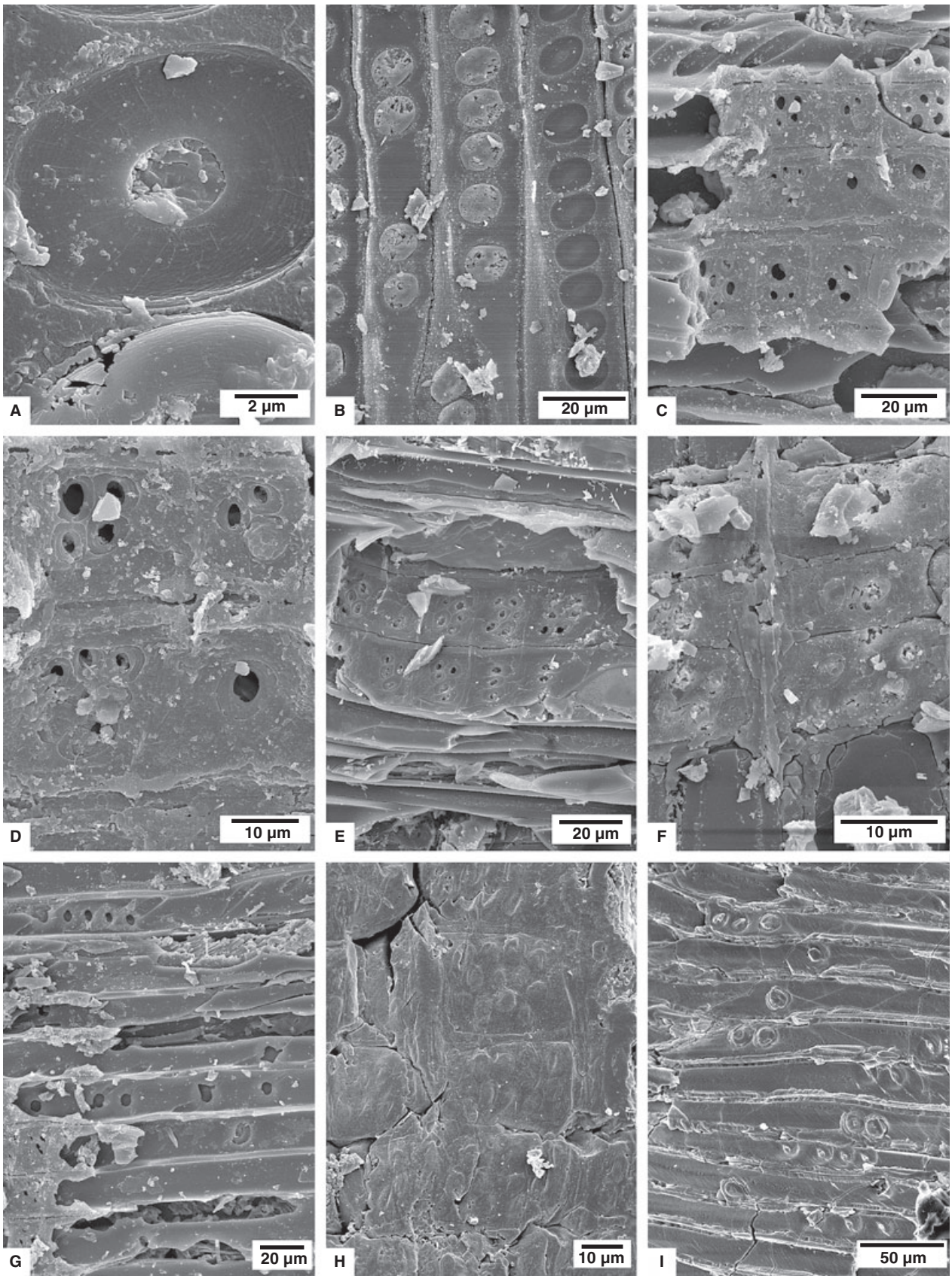
Determination. Specimens can be assigned to the morphogenus *Brachyoxylon* Hollick and Jeffrey, because they display araucarioid cross-fields and mixed to araucarian radial pitting (Philippe 1993; Bamford and Philippe 2001; Philippe and Bamford 2008), although the cross-field pitting variability is really outstanding, without equivalent among described *Brachyoxylon* morphospecies to the best of our knowledge. The anatomical features fit well with those given in the *Protocupressinoxylon purbeckensis* protologue (i.e. original diagnosis, description, illustrations and taxonomical and nomenclatural comments of the author) by Francis (1983). The original diagnosis did not mention cross-field pitting variability, but this was convincingly illustrated elsewhere in the protologue (Francis 1983, pl. 39, fig. 6, and text-fig. 3). Our specimens differ from the British material in having alternate or sub-opposite biseriate pitting on the tracheid radial wall, whereas the latter is said to have only opposite biseriate pitting (this feature is not illustrated in the protologue). In wood of mixed type, the radial pitting was usually very variable, but we think this variability is of little taxonomical significance. The pitting we observed on the tracheid radial walls is also less araucarian compared to British specimens, but again this is a variable feature, strongly influenced by tracheid width and probably wood ontogenetic age.

Fossil wood is distributed within morphospecies and morphogenera, which do not fit perfectly with usual Linnaean taxa. In other words, two fossil wood specimens assigned to the same morphospecies could originate from different biological species (because of the conservative nature of wood structure). In our case, it must be noted, however, that the type of cross-field pitting we observed has never been found anywhere in Jurassic and Cretaceous strata, except for during a short time interval (Kimmeridgian–Tithonian) and in a limited area (south-western Europe) (see 'distribution' below). Our specimens probably all belong to the same biological species, or a set of closely related ones.

Taxonomical and nomenclatural notes. Among Jurassic wood species previously described, highly variable early wood cross-field pitting is rare. Even if in some species the number of pits per cross-field is variable, cross-field pit size is usually constant. It is thus noticeable that, among our specimens, isolated cross-field oculipores were distinctly larger and that even within a single cross-field the oculipore diameter was variable. In recent conifers, this condition is known only in some members of the Araucariaceae (Greguss 1955, pls 3, 8). Our specimens are also related to this family, because cross-field pits are usually contiguous and alternate oculipores (Süß and Schultka 2006). Radial pitting in our specimens, however, clearly belongs to the mixed type, whereas modern Araucariaceae display exclusively araucarian radial pitting. For contemporaneous wood from Tanzania, also with araucarioid cross-fields and mixed type of radial pitting, Süß and Schultka (2006) have proposed a systematic position intermediate between the Podocarpaceae and Araucariaceae. As for most of the Jurassic wood specimens, assignment to a modern family is hypothetical.

There is a nomenclatural problem with *Protocupressinoxylon* Eckhold. This morphogenus is a junior nomenclatural synonym of *Protobrachyoxylon* Holden (Philippe 1993) (but not of *Paracupressinoxylon* Holden; Philippe and Bamford 2008). Thus, and despite that *Protocupressinoxylon* was frequently used, it is illegitimate. Conservation has never been proposed for this genus. Several problems prevented the proposal of such a conservation. First, all material for *Protobrachyoxylon eboracense* Holden, the type species of the genus *Protobrachyoxylon*, has been lost (Philippe 2002). Second, from the elements given in *P. eboracense* protologue, genus *Protobrachyoxylon* is very probably a taxonomical synonym of *Brachyoxylon* Hollick and Jeffrey, and thus genera *Protocupressinoxylon* and *Brachyoxylon* are very probably taxonomical synonyms. Third, *Protocupressinoxylon* Eckhold has been used in very different ways, depending on whether authors paid more attention to one or another of

TEXT-FIG. 6. *Protocupressinoxylon purbeckensis* Francis – wood anatomy. A, detail of an areolate pit chamber. B, mixed type of pitting on radial tracheid wall. C, ray in radial view. D, details of four cross-fields, note the variable oculipores size and number per field. E, other cross-fields, looking more typically araucarioid. F, cross-fields in radial view, with variable pit size and number. G, mixed type of pitting on radial tracheid wall. H, typical araucarioid cross-fields. I, mixed type of pitting on radial tracheid wall. A–E, JT-20 (Spain); F–G, MJSN TCH005-322 (Switzerland); H–I, LPUL MP403 (Switzerland).


A
2 µm
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E
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F
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G
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H
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the Eckhold's syntypes or to Eckhold's diagnosis (which unfortunately does not described oculipore arrangement in cross-fields). Fourth, the genus *Protopodocarpoxylon* Eckhold was often used for material with araucarioid cross-fields and mixed-type of radial pitting (just as in *Brachyoxylon* Hollick and Jeffrey), in line with the condition observed by the type material for *Cedroxylon blevillense* Lignier, one of the *Protopodocarpoxylon* Eckhold syntypes (Lauverjat and Pons 1978).

A nomenclatural and taxonomical reappraisal of Mesozoic wood genera is currently in progress by one of us. Meanwhile, we will use herein the name *Protocupressinoxylon purbeckensis* Francis, which is well known and based on well-described material (Francis 1983).

Fossil wood compilation for southwestern Europe at the Jurassic/Cretaceous boundary. The results of our compilation are given in Table 2. Some entries need explanations. In 1953, Grambast assigned a wood from Berriasian sands of the Pays de Bray (France) to *Xenoxylon phyllocladoides* Gothan. This generic assignment has been rejected (Philippe and Thévenard 1996), and even though we have not yet reviewed the original specimen, we provisionally rename it *Circoporoxylon* sp. on the basis of Grambast's illustration. Moreover, the specimen Grambast studied was silicified and found within sands that also included reworked material. This fossil wood might thus be reworked from the underlying Tithonian sediments and be the same wood type as the one mentioned as *Circoporoxylon* sp. by Francis (1983) from contemporaneous deposits of the Isle of Portland in Dorset.

In 1981, Barale described two *Cupressinoxylon* (sp. A and sp. B) from the Kimmeridgian of Southern Jura, which are anatomically similar to *Protocupressinoxylon purbeckensis*. Both have variable cross-field pitting, sometimes featuring only one oculipore per field, but these single oculipores are not larger than usual. These woods were re-assigned to *Brachyoxylon* (Philippe, 1995). Meyer (1994) mentioned the occurrence of *Agathoxylon desnoyersii* in the Upper Kimmeridgian of Soleure (Switzerland). Further investigations into the original specimen with Collodion microcasts and SEM indicated that the wood from Soleure is a *Brachyoxylon* sp. (up to 12 oculipores per field, long araucarian chains of biseriate alternate pits on radial tracheid walls, see Text-fig. 6H–J), which clearly differs from *Protocupressinoxylon purbeckensis*. The wood flora described by Valenzuela *et al.* (1998) from the Kimmeridgian of Asturias (Lastres Fm.) featured *Protocupressinoxylon* sp. and *Agathoxylon* sp. It is difficult to judge the relationships between their *Protocupressinoxylon* sp. and *P. purbeckensis*, as there are some discrepancies between text and illustrations, but the cross-field illustrated in the middle of their figure (Valenzuela *et al.*1998, fig. 8D) is strongly reminiscent of the latter species. The review by one of us (M.P.) of the Mesozoic fossil wood stored in the palaeobotanical collections at the Natural History Museum, London, yielded relevant data.

DISCUSSION

Distribution of Protocupressinoxylon purbeckensis

The record of *P. purbeckensis* in the literature is limited. After its first mention by Francis (1983), it was discovered in the Kimmeridgian of Dorset (Abineri 1989). Some wood from the Cretaceous of Namaqualand was tentatively referred to this taxon (Bamford and Corbett 1994), but review of the original slides (stored in Bernard Price Institute, Witwatersrand University, Johannesburg, South-Africa) did not show either cross-fields with a single large oculipore or variable oculipore size.

A number of wood specimens with araucarioid cross-field pitting and a mixed type of radial pitting (so-called *Brachyoxylon*-type) have been described from the Late Jurassic or Early Cretaceous all around the world. However, it must be pointed out that *Brachyoxylon* wood-type does not have a lot of characteristic features that morphospecies are all similar within that morphogenus and that limited observations could lead to wrong conclusions. We consider it diagnostic that in both the Swiss and the Spanish material, as well as in the type specimen of *Protocupressinoxylon purbeckensis*, when an oculipore occurs singly in a cross-field, it was always much larger than multiple pits. However, single-pitted cross-fields could have been overlooked in some wood specimens mentioned in the literature, as such cross-field pitting was present in only about 5% of the observed cross-fields in our specimens.

Only two similar morphospecies were reported from the latest Jurassic – earliest Cretaceous of Western Europe, namely *Brachyoxylon trautii* (Barale) Philippe and the briefly described *Prototaxodioxylon* sp. Mohr and Schultka. The first species, *Brachyoxylon trautii*, is distributed from the Bathonian to the Kimmeridgian in Western Europe (Philippe 1995, and several unpublished data). The species is known by tens of well-preserved samples, and oculipores are never larger than usual when occurring singly in a cross-field. The wood described as *Prototaxodioxylon* sp. by Mohr and Schultka (2000) originated from the famous Kimmeridgian lignite mine in Guimarota (Portugal). Because of close provenance and similar palaeoenvironmental setting and age, we suspected that this Guimarota wood could be conspecific with our Spanish material. On our request, Stephan Schultka kindly performed more investigations into this Guimarota wood and, despite careful searching, was unable to find any

TABLE 2. Fossil wood record at Jurassic/Cretaceous boundary in Western Europe.

Source	Determination	Locality	Age	Sedimentological setting
MP856, MP1284, MP1285	*Brachyoxylon trautii*	Pagny-sur-Meuse (55)	Late Oxfordian, Bifurcatus zone	Tidal channel in reefal setting
MP1286	*Agathoxylon*	Pagny-sur-Meuse (55)	Late Oxfordian, Bifurcatus zone	Washover deposits
MP1095	*Agathoxylon desnoyersii*	Les Pezières (01)	Late Oxfordian, late Bifurcatus Zone	Offshore marls
MP533	*Agathoxylon*	Montalieu (38)	Late Oxfordian, Bimmamatum zone	Offshore limestones
Garcia *et al.* (1998)	*Agathoxylon*	Meuilley (21)	Late Oxfordian	Offshore
Philippe (1995)	*Brachyoxylon trautii*	Loulle (39)	Late Oxfordian, Planula zone	Tidalites in perireefal succession
Weidman (1972)	*Agathoxylon*	Chablais (74)	Late Oxfordian	Offshore
Barale (1981)	*Brachyoxylon*	Virieux-Martin (01)	Early Kimmeridgian	Perireefal
MP1769, MP1770, MP1771	*Agathoxylon*	Villerville (14)	Early Kimmeridgian	Offshore marls
MP289	*Brachyoxylon* sp.	Savigny-le-sec (21)	Early Kimmeridgian	Perireefal
Creber (1972)	*Piceoxylon*	Helmsdale, East Sutherland (UK)	Kimmeridgian	Marine breccia
Seward and Bancroft (1913)	cf. *Piceoxylon* (given as *Cedroxylon hornei*)	Helmsdale, East Sutherland (UK)	Kimmeridgian	Marine breccia
Creber (1972)	*Piceoxylon*	Sandringham Sands, Norfolk (UK)	Kimmeridgian	Marine sands
Abineri (1989)	*Protocupressinoxylon purbeckensis*	Kimmeridge Clay, Dorset (UK)	Kimmeridgian	Marine environment
NHML 40540	*Agathoxylon*	Kimmeridge Clay, Weymouth (UK)	Kimmeridgian	Marine environment
NHML 2408	*Protocupressinoxylon*	Devizes, Wiltshire (UK)	Kimmeridgian	Not described
Mohr and Schultka (2000)	*Protaxodioxylon* (given as *Prototaxodioxylon*)	Guimarota (Portugal)	Kimmeridgian	Coastal swamp
Valenzuela *et al.* (1998)	*Protocupressinoxylon* sp.	Asturias (SP)	Kimmeridgian	Deltaic (fluvial-dominated)
This study	*Protocupressinoxylon purbeckensis*	Asturias (SP)	Kimmeridgian,	Deltaic (fluvial-dominated)
MP1030	*Brachyoxylon trautii*	Georges du Verdon (83)	Late Kimmeridgian	Reefal limestones
MP1183	*Brachyoxylon* cf. *trautii*	Bure (55)	Late Kimmeridgian	Oyster rich marls
Barale (1981)	*Brachyoxylon* sp.	Cerin (01)	Late Kimmeridgian	Perireefal
This study	*Protocupressinoxylon purbeckensis*	Courtedoux, Jura (CH)	Late Kimmeridgian Eudoxus zone	Offshore oyster rich marls
MP403	*Brachyoxylon* cf. *trautii*	Soleure (CH)	Late Kimmeridgian	Shallow sub-tidal lagoon
MP639	*Circoporoxylon*	Cran Barbier (62)	Earliest Tithonian	Offshore marls
MP1184, MP1589	*Agathoxylon*	Cap Gris-Nez (62)	Earliest Tithonian	Marls
MP968, MP1159	*Agathoxylon*	Ile d'Oléron (17)	Tithonian	Proximal marls
MP1290	*Protocupressinoxylon*	Ile d'Oléron (17)	Tithonian	Proximal marls
NHML V8384	*Agathoxylon*	Portland	Tithonian	Unknown
NHML V7513	*Agathoxylon*	Portland	Tithonian	Unknown
Grambast (1953)	*Circoporoxylon*	Sully (60)	Late Tithonian, Anguiformis zone, possibly reworked	Marine sands
Francis (1983)	*Agathoxylon*	Isle of Purbeck (UK)	Latest Tithonian	Palaeosoil with calcrete
Francis (1983)	*Circoporoxylon*	Isle of Purbeck (UK)	Latest Tithonian	Palaeosoil with calcrete
Francis (1983)	*Protocupressinoxylon purbeckensis*	Isle of Purbeck (UK)	Latest Tithonian	Palaeosoil with calcrete
Stockholm P50	*Taxodioxylon*	Portland (UK)	Latest Tithonian	Unknown

TABLE 2. (*Continued*).

Source	Determination	Locality	Age	Sedimentological setting
NHML 24809	*Circoporoxylon*	Tisbury, Wiltshire (UK)	Latest Tithonian	Unknown
NHML V18882	*Circoporoxylon*	Seacombe, Dorset (UK)	Latest Tithonian	Unknown
MP641	*Protocupressinoxylon* sp.	Pointes aux oies (62)	Latest Tithonian – Early Berriasian	Tsunami deposit (Schnyder *et al.*, 2005*a*)
MP1182	*Agathoxylon*	Pointes aux oies (62)	Latest Tithonian – Early Berriasian	Tsunami deposit (Schnyder *et al.*, 2005*a*)
Philippe *et al.* (2008)	*Agathoxylon*	Wimereux (F)	Early Berriasian	Unknown
Philippe *in* El Albani *et al.* (2004)	*Agathoxylon*	Cherves (16)	Berriasian	Shallow-water inner latform to lagoon
Ward (1896)	*Agathoxylon*	Portland (UK)	Berriasian	Not described

When a number like 'MPxxxx' is given as the source, it is a new data; numbers like 'NHML xxxx' refer to specimen xxxx of Natural History Museum, London, UK. Number given between brackets after a locality refers to French *département* (administrative unit) number. Sedimentology from Olivier *et al.* (2004), Schnyder *et al.* (2005*a*) and references in the text.

cross-field with a single large oculipore (S. Schultka, pers. comm. 2007).

In the Purbeck Formation (England), *P. purbeckensis* was found associated with the foliage *Cupressinocladus valdensis* (Seward) Seward (Francis 1983). This morphospecies has not yet been found from the Late Jurassic strata of the Jura Mountains, despite Kimmeridgian levels in that region yielding rich and diverse palaeofloras (Barale 1981). Similar species of *Cupressinocladus* (*C. itieri* (Saporta) Barale, *C. strobilifer* (Schimper) Barale), however, were recorded from the Late Kimmeridgian of Southern Jura (Barale 1981). In the Purbeck Formation, *P. purbeckensis* is associated with male cones named *Classostrobus* and with *Classopollis*-type pollen (Francis 1983). Both *Classostrobus* and *Classopollis* are frequent in the Late Kimmeridgian of the Jura Mountains. The relationships between these different types of fossils are not specific enough, however, to allow safe inferences about their respective distributions, all the more since they are implied in different taphonomical processes (Barale and Courtinat 1980).

Palaeoecology of Protocupressinoxylon purbeckensis

The seminal study by Francis (1983) demonstrated that the wood *Protocupressinoxylon purbeckensis*, the foliage *Cupressinocladus valdensis* (Seward) Seward, the male cone *Classostrobus* sp. and the pollen *Classopolis* sp. all came from one fossil tree type belonging to the Cheirolepidiaceae (Watson and Alvin, 1999), an extinct family of conifers. On the Isle of Portland during the Late Jurassic, the *P. purbeckensis* tree grew in a thin soil with calcrete, in a terrestrial environment but at the edge of a shallow hypersaline lagoon, under a strongly seasonal climate. Together with some cycadophytes, this conifer built closed forests, where some logs reached over 13 m in length and 1.3 m in diameter (Francis 1983). Some trunks branched about 6 m above ground level (Fitton 1836). Two other wood types (*Agathoxylon* and *Circoporoxylon*) were found associated with *Protocupressinoxylon purbeckensis* in the Purbeck strata, but these were much rarer (three specimens only, <10% of the total, Francis 1983). From a range of proxy sources, Francis (1984) came to the conclusion that the climate was semi-arid, with mean annual rainfall of about 400–700 mm, falling mainly during the winter months. As a similar modern environment, she proposed Rottnest Island in Western Australia where natural stands of *Callitris preissii* Miq. trees live adjacent to ephemeral salt lakes.

When found on the Isle of Portland, *Protocupressinoxylon purbeckensis* was rooted within well-developed palaeosoils (Francis 1984). In Asturias, *P. purbeckensis* probably also grew on calcareous soils, because carbonated soft-pebbles were commonly found associated with the fossil wood: carbonate-rich soils, similar to those known in the underlying Vega Formation, probably occurred up-stream during the deposition of Lastres Formation. *Protocupressinoxylon purbeckensis* has never been found in reefal and perireefal environments. The anatomically similar, common and widespread contemporaneous species *Brachyoxylon trautii* has never been found associated with *Protocupressinoxylon purbeckensis*. Throughout its Bathonian to Kimmeridgian range, *B. trautii* has always been found in association with reefal or perireefal environments (Philippe 1995; Garcia *et al.* 1998). When found *in situ*, e.g. in the Oxfordian of Charbonnières (Doubs, France; Philippe 1995), the roots of *B. trautii* were observed within oolithic sand bars, tidalites or sublithographic limestones.

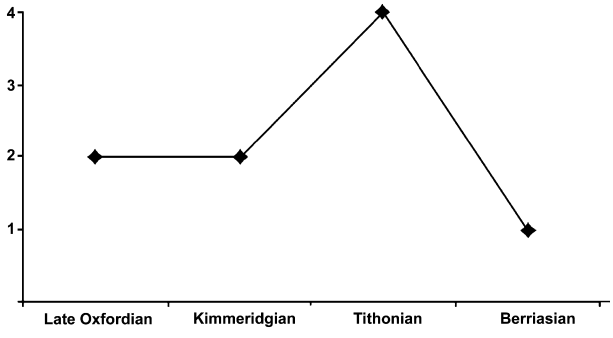
From our fossil wood record for the Late Jurassic of southwestern Europe (with about 200 data), these two wood species seem to be exclusive. Tolerance to haline conditions (sea spray or haline soil) could explain this

pattern, with *B. trautii* being more halophytic and *P. purbeckensis* being less salt tolerant. From the size of the fossil wood remains, in particular the Swiss branches, it is clear that *P. purbeckensis* was a sizeable tree, as already indicated by Francis (1984) in England. It grew on well-developed carbonate-rich soils (rendosols to calcosols). In contrast, *B. trautii* was a rather small tree, pioneering on sand dunes (Barale *et al.* 1991). From our observations, we conclude that, despite the low and flat topography that largely prevailed over southwestern Europe at Jurassic/Cretaceous boundary, at least two coastal ecosystem types with trees might have existed.

Southwestern European wood flora at the Jurassic/Cretaceous boundary

Fossil wood floras of the considered period and area are not diverse (Text-fig. 7). Indeed, despite the wide range of sedimentological settings, only six morphogenera have been reported (*Agathoxylon*, *Brachyoxylon*, *Circoporoxylon*, *Piceoxylon*, *Protaxodioxylon*, *Taxodioxylon*; the *Protocupressinoxylon* data in Table 2 are considered as congeneric with those for *Brachyoxylon*). This does not compare with, for example, the Toarcian period, for which a dozen morphogenera are known for the same area (Philippe 1995, 2000). The low generic diversity from southwestern Europe from the Late Oxfordian to Tithonian interval supports the proposal of a (at least seasonally) very dry climate (Francis 1984; Ruffell *et al.* 2002; Riboulleau *et al.* 2007). Diversity rose from the Late Oxfordian to the Tithonian, possibly indicating temporary wetter snaps, before collapsing during the Berriasian. After the Berriasian wood diversity rose again (Philippe *et al.* 2008).

Francis (1984) convincingly demonstrated that *P. purbeckensis* tree grew under strongly seasonal semi-arid climate of Mediterranean type. It appeared in the fossil record during the Kimmeridgian and lingered during the Tithonian. The disappearance of *P. purbeckensis* at the end of the Tithonian, together with the collapse of wood generic diversity, could indicate a strong climatic perturbation at the Jurassic/Cretaceous boundary in southwestern Europe. Accordingly, such a sharp climatic change would have deeply affected terrestrial biocoenoses. Drought-stressed vegetation usually yields lower primary production, and this could have in turn restricted animal diversity and simplified terrestrial food webs, especially among tetrapod communities.



TEXT-FIG. 7. Fossil wood generic diversity during the late Oxfordian – Berriasian interval in southwestern Europe. Data source is Table 2.

There is, however, some similarity between the curve in Text-figure 7 and the one given 20 years ago by Benton (1987, fig. 1) for the evolution of nonmarine tetrapod (amphibians, reptiles, birds, mammals) diversity (at family level) over the same time interval. Nevertheless, a recently updated nonmarine tetrapod diversity curve does not show any decrease at Jurassic/Cretaceous boundary (Fara and Benton 2000). New investigations showed that the apparent fall in nonmarine tetrapod biodiversity during the earliest Cretaceous may be explained by a failure in preservation linked to a sharp switch from marine to continental deposition at that time in Europe (Hallam and Wignall 1997), and by a fossil *Lagerstätte* effect at the end of the Jurassic (Benton 1995). The sharp decrease we observed for wood diversity at Jurassic/Cretaceous boundary might be driven by climatic change, but might also result from a preservation bias.

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